

# Allometric Patterns of Cranial Bone Thickness in Fossil Hominids

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**ABSTRACT** The interspecific allometry of five measures of total cranial bone thickness is examined in 10 extant catarrhine genera and two fossil hominid samples representing *A. africanus* and Asian *H. erectus*. Analysis of the modern sample shows that most interspecific variation in vault thickness can be accounted for by variation in body size. Correlation values are moderate to high ( $r = 0.75\text{--}0.98$ ), and all variables exhibit positive allometry. The bone thickness:body mass relationship of modern humans broadly conforms with that of other primates. However, in the distribution of relative thickness throughout the skull, *H. sapiens* is distinguished by relative thickening of the parietal and extreme relative thinning of the temporal squama. The bone thickness:body mass relationship in the two early hominid species is examined using published mean body weight estimates generated from post-cranial predictor variables. *A. africanus* exhibits great similarity to modern humans in its relation to the catarrhine regression data and in the distribution of relative thickness throughout the skull. *H. erectus* also shows a modern human-like pattern in the distribution of its relative thickness; however, its bone thickness:body mass relationship is dissimilar to that displayed by all other taxa, including the other hominid species. On the basis of these results, it is suggested that the published body weight estimate assigned to *H. erectus* greatly underestimates actual mean body size for Asian members of this species. © 1996 Wiley-Liss, Inc.

Many pre-Holocene populations of the genus *Homo* display mean cranial thickness values that equal or exceed the maximum population averages characterizing recent *H. sapiens* (Brown, 1987). These differences have led researchers to conclude that, relative to anatomically modern humans, the species *H. erectus* and archaic populations of *H. sapiens* exhibit greatly thickened cranial bone (e.g., Morant, 1938; Twisselman, 1941; Weidenreich, 1943, 1951; Howells 1966, 1980; Trinkaus and Howells, 1979; Murrill, 1981; Wolpoff, 1984; Kennedy, 1991). Because of its differential distribution, cranial thickness is often cited as a relevant trait in cladistic analyses, which rely on the distribution of autapomorphic and synapomorphic character states to establish species' identity

and relationships (Delson et al., 1977; Andrews, 1984; Stringer, 1984; Wood, 1984; Bilsborough and Wood, 1986; Hublin, 1986; Turner and Chamberlain, 1989). Indeed, some researchers suggest that the thickened cranial and/or postcranial bone found in some early hominids may represent a unique condition among anthropoids (Weidenreich, 1943) or all mammals (Kennedy, 1985).

In addition to examining its purported taxonomic significance, several studies have sought to identify the factors underlying the considerable range of cranial thickness variation characterizing modern humans. These investigations have provided valuable infor-

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mation by documenting differences within populations and describing the effects of age, sex, and pathology on thickness variation (e.g., Roche, 1953; Israel, 1973, 1977; Tallgren, 1974; Adeloje et al., 1975; Brown et al., 1979; Ortner and Putschar, 1985; Smith et al., 1985; Brown, 1987; Ishida and Dodo, 1990). However, their results have been of limited usefulness in the development, or testing, of functional explanations for population or species level differences in bone thickness. In part, this is due to a lack of comparability between studies that are methodologically not consistent; but more importantly, it can be explained by the lack of necessary correspondence between factors producing intra- and interclass variation. Nevertheless, over the years, several hypotheses have emerged to explain interspecific, diachronic changes in hominid cranial thickness. For example, Wolpoff (1980) and Tappen (1969) argue that thick cranial bone was selectively advantageous to early *Homo* because it provided protection from predation or intraspecifically inflicted traumatic injury. Alternatively, Weidenreich (1943), Tobias (1967), and Nawrocki (1991) propose that a biomechanical interaction between changing skull shape, mediated by brain expansion, and masticatory stress factors is responsible for differences in hominid vault thickness. Still others conclude that cranial and postcranial bone thickening in some hominid populations reflects the presence of significant functional differences in the hormonal and endocrine systems that control metabolic processes (Lovejoy, 1982; Kennedy, 1985; Hublin, 1986; Ivanhoe and Hammel, 1990).

Although variation in hominid vault thickness has been carefully documented and its functional etiology in *H. sapiens* has been widely discussed, research has seldom extended outside the family. Because of this lack of comparative data, there is no way of knowing whether primate species are characterized by consistent patterns of interspecific variation in cranial thickness; whether patterns of thickness in hominid species are concordant with other primates; or whether deviations from typical patterns of cranial thickness occur with predictable regularity. In particular, the interspecific relationship between cranial thickness and body size has

never been investigated, despite the fact that there is evidence for such an association. Among extant primates, postcranial variables that measure bone thickness, such as femoral cortical cross-sectional area, are highly correlated with body mass and are considered among the strongest predictors of weight (Ruff, 1987, 1989; Smith, 1993a; Nelson, 1994). Moreover, several cranial metric variables are known to be highly correlated with mass (Aiello and Wood, 1994). The strength of their relationship is surprising, since the skull does not participate in overall support of the organism and is thus somewhat removed from the design constraints produced by the interaction between gravity and body size (Jungers, 1990).

Recognizing that a broad, comparative perspective is essential in interpreting the phylogenetic relevance and adaptive significance of evolutionary changes in any trait, this study is centered on an interspecific analysis of cranial thickness and body size in a series of modern primate taxa and two fossil hominid species, *Australopithecus africanus* and *H. erectus*. The static allometric data (Gould, 1966; Calder, 1984) are used in two ways. First, the interspecific scaling relationship between measures of cranial thickness and mass is delineated in extant catarrhines. Fossil hominids are evaluated against this comparative framework, using published body weight estimates to represent each species. Second, the residual data, which represent variance unaccounted for by size, are examined. The distribution of relative thickness throughout the cranial vault is compared among all taxa. Together, these data are used to determine whether consistent patterns of cranial thickness are present in either the modern or fossil samples. Isolating such interspecific patterns of variance will provide greater resolution to the descriptive data on early hominid cranial thickness which, in turn, will contribute to an increased understanding of both the functional and taxonomic significance of the character.

## MATERIAL AND METHODS

### The sample

The extant comparative sample consists of 235 adult crania representing 14 catarrhine

species (*C. aethiops*, *C. mitis*, *C. nictitans*, *C. guerza*, *C. gorilla*, *H. sapiens*, *H. agilis*, *H. klossii*, *H. lar*, *H. sundactyles*, *M. nemes-trina*, *P. troglodytes*, *P. cynocephalus*, *P. pyg-maeus*). Data for nonhuman primates was compiled from wild-shot specimens housed at the United States National Museum of Natural History, Los Angeles County Museum of Natural History, University of California Museum of Vertebrate Zoology, and Department of Anthropology, University of California, Santa Cruz. Modern *H. sapiens* is represented by crania from coastal and inland Californian, Japanese, and Fijian archaeological populations. This material is curated to the Fowler Museum of Cultural History, University of California, Los Angeles. Whenever possible, the adult status of each modern specimen was ascertained using both postcranial epiphyseal closure and third molar eruption. To control for age-related or pathological conditions that can effect changes in bone thickness during adulthood, individuals exhibiting visible evidence of chronic disease or trauma (other than injuries related to death) were eliminated from the sample (Baer, 1956; Moseley, 1963; Israel, 1973, 1977; Ruff, 1980; Frame et al., 1987). The influence of age on sample variation was examined by classifying individuals into one of three broad age categories, based on molar wear patterns. These groups were evaluated using an analysis of variance with a Tukey's HSD t test. Because no significant differences were detected ( $P < 0.01$ ), the entire primate sample is treated as a single age unit.

The fossil sample, detailed in Table 1, represents two important geographic and temporal foci in hominid evolution. Pliocene remains from Africa are represented by cranial specimens of *A. africanus* from Sterkfontein and Makapansgat. In addition to the better known individuals of this taxon, this subsample includes several undescribed fragmentary specimens from Sterkfontein which, at the time of examination in 1989, were listed as deriving from either Member 4 or 5 (StW-185, 262, 299, 316, 498). It should be noted that attribution of the entire South African subsample to *A. africanus* is somewhat problematic, given the uncertain stratigraphic context and fragmentary nature of many specimens. Moreover, the spe-

TABLE 1. Fossil hominid sample and individual cranial bone thickness measurements<sup>1</sup>

	MF	BR	MP	MT	OC	Source <sup>3</sup>
<i>A. africanus</i>						
TM 1511				4.9	10.0	1,2
Sts 5	5.0	6.1		5.5	12.7	1
Sts 19				6.4	10.1	1
Sts 25		7.5		7.3	9.3	1
Sts 26			7.2		8.7	1
Sts 71	8.3	7.0		4.2	11.8	1,2
MLD 1					15.0	1
StW 13	7.0		5.8	5.2		1,2
StW 185		6.0 <sup>1</sup>				1
StW 187b					12.5	1
StW 252a-s	6.8	5.0	6.1			1
StW 262					10.6	1
StW 299			5.4			1
StW 316			6.9			1
StW 498	6.4	5.0				1
<i>H. erectus</i>						
Trinil 2	7.0	9.0 <sup>1</sup>	9.0		15.0	3
S 2	9.0	9.0 <sup>1</sup>	12.5	8.0	20.4	3
S 4			11.5	7.0	21.5	3
S 10	6.5	8.9	11.2	4.7	15.2	1
S 12	7.1	8.8	9.1	4.7	20.9	1
S 13a			10.0			4
S 17	6.3	10.4	9.5	5.4	28.2	1
S 18a		11.0 <sup>1</sup>	10.5			4
SB7904b			7.7 <sup>2</sup>			1
Ng 1	7.1	8.0	7.9	2.9	18.8	1
Ng 3	11.1	11.0	11.7		12.7	1
Ng 5	6.7	8.2	8.5			1
Ng 6	6.9	10.5	9.5	5.6	25.6	1
Ng 9			9.2			1
Ng 10	9.0					1
Ng 11	9.0	8.9	10.2	6.0	24.3	1
Ng 12	6.5	7.9	11.8	6.0	32.2	1
Sk I	13.0					3
Sk II	10.0	9.0 <sup>1</sup>	11.0	10.0		3
Sk III	10.0	9.6 <sup>1</sup>	11.0	9.3	20.4	3
Sk V				10.0	12.3	3
Sk VI	9.5	9.9 <sup>1</sup>	11.2	7.7		3
Sk X	7.0	7.5 <sup>1</sup>	12.5	5.2	15.0	3
Sk XI	11.0	7.0 <sup>1</sup>	16.0	6.0	12.0	3
Sk XII	7.0	9.7 <sup>1</sup>	9.0	7.0	15.0	3

<sup>1</sup> Measurement taken on parietal.

<sup>2</sup> Measurement taken posteriorly.

<sup>3</sup> Sources for the data are: 1, this study; 2, Tobias, 1991; 3, Weidenreich, 1943; and 4, Jacob, 1973.

cies' integrity of remains from Member 4 has been challenged recently (Kimbel, 1991; Kimbel and White, 1988; Clarke, 1988), although to date no systematic revision of the species has been published. Unfortunately, the sample size and fragmentary condition of the fossils precludes an examination of intragroup variation in measures of cranial thickness.

*H. erectus* is represented by a geographically diverse, but morphologically homogeneous, group of fossils from the Asian mainland and island of Java. Although a few workers have advocated complex taxonomic interpretations of this material (Coon, 1862;

Jacob, 1975; Sartono, 1982), most researchers favor attribution to a single species (Weidenreich, 1951; Santa Luca, 1980; Pope, 1983; Rightmire, 1990). The subsample includes Chinese specimens from *Zhoukoudian*, Locality 1, and Indonesian material derived principally from the Kabus and Notojuro Formations. Despite the considerable confusion surrounding the age of many Asian hominids (Swisher et al., 1994; DeVos, 1994) there is general agreement that all but one of the *H. erectus* crania in this study (S4) date to the middle Pleistocene (Pope, 1983, 1988; Semah, 1984; Wu, 1985; Theunissen et al., 1990). The precise age of the *Pithecanthropus* IV skull, which is associated with the uppermost layers of the Pucangan Formation, is unknown. However, it is most certainly younger than the 1.66 Ma age recently proposed for the lower horizon of this formation (de Vos, 1985; Swisher et al., 1994). The *H. erectus* subsample includes only one previously undescribed specimen, SB7904b, a left parietal fragment from the Sangiran Dome area (Gauld et al., in press).

### Data collection

An inherent problem in comparative allometric studies that include fossil samples involves the choice of a variable to represent size. One possibility is to employ an osteometric reference variable as a substitute for size; however, the disadvantage to this strategy is that the true scaling relationship of the feature in question can be obscured, if the relationship between size and the intervening variable is not perfectly isometric (Smith, 1981; Hartwig-Scherer and Martin, 1992). The advantage to this method is that the same variables can be examined across all taxa. The alternative strategy is to use the most reliable and relevant measure of size, body mass, which is commonly represented as body weight (Calder, 1984; Schmidt-Nielsen, 1984). The disadvantage here involves the use of indirectly derived weight estimates for fossils, which again introduces the error and distortion associated with intervening variables. Despite its drawback, this method was judged preferable for the purposes of this study because it allowed a more direct comparison of the relationship between cranial thickness and size in the

extant sample, where body weight information was available.

Catalogued weights were available for 120 modern primate specimens (59% of the non-human reference sample). Individuals lacking a recorded body weight were assigned a species-specific sex mean value based on published data (Harvey et al., 1987; McHenry, 1988; Jungers, 1988). Body mass estimates for the human archaeological sample were generated from intraspecific formulae for three statistically reliable predictors of human body weight: femoral subtrochanteric area, femoral head diameter, and proximal tibial articular area (McHenry, 1992). The value assigned to each individual was calculated as the mean of all available estimates. Comparison of these predicted values with published data suggests that the estimates fall within the range of weights characterizing modern indigenous populations from the same geographic regions (Roberts, 1953; Eveleth and Tanner, 1990).

The weight estimates assigned to each fossil hominid species were derived from the literature. Several studies have examined body size in australopithecines (e.g., Robinson, 1972; McHenry, 1974, 1975, 1976, 1991, 1992; Gingerich et al., 1982; Jungers, 1982, 1988, 1990). While the entire range of predicted weights provided by these studies is quite broad (20.0–67.5 kg), the results of recent analyses, based on predictor variables whose reliability has been critically assessed, tend to converge (Jungers, 1988, 1990; McHenry, 1988, 1992). The mean body weight assigned to *A. africanus* represents the average of two estimates (35.5 and 44.8 kg), compiled from regression data for measures of hindlimb joint size (McHenry, 1992). The 40.5 kg value falls close to the midpoint for the entire range of values that have been presented in the literature (Gauld, 1992). In comparison to australopithecines, very few studies have addressed body weight estimation among Pleistocene hominid populations. Asian *H. erectus* is assigned a mean body weight value of 48.0 kg. This represents the average of individual estimates reported by Rightmire (1986), who used modern human femoral cross-sectional area to predict individual body weights for three "*Pithecanthropus*" and four "*Sinanthropus*" postcrania.

nial specimens. More recently, McHenry (1988), Ruff and Walker (1993), and Aiello and Wood (1994) have produced higher estimates (range = 58.6–91.2 kg) for early African *H. erectus*; however, because of the suggestion that the species may exhibit geographic variability in body shape and size, these estimates are not included in the calculation of Asian *H. erectus* body weight (Ruff, 1991).

In addition to body mass, the study utilizes five primary thickness variables (Fig. 1). Their selection was based on the need to sample bone thickness throughout the cranial vault at points that were homologous across taxa, and comparable to measurement points described by other researchers (Gauld, 1992). Two variables are located at positions dominated by sutures or superstructural development. Bregmatic thickness (BR) was measured on the most posterior point of the frontal bone at the junction of the coronal and sagittal sutures; maximum thickness of the occipital bone (OC) was taken in the cranial midline. Three variables, representing generalized thickness, are located on the squamous portions of the frontal, temporal, and parietal bones, in areas of the vault unaffected by sutures or superstructures. Midfrontal thickness (MF) was measured at the midpoint of the frontal chord. In specimens exhibiting development of internal and/or external superstructures, MF thickness was moved to a lateral position. Midparietal thickness (MP) was measured at the intersection of lines dividing the bone into four approximately equal quadrants. The measurement point was adjusted minimally to avoid involvement of the temporal crest or meningeal grooves. Midtemporal thickness (MT) was taken at the midpoint of a line, drawn perpendicular to the Frankfort plane, from auriculare to the external edge of the suture. All measurements were made perpendicular to a tangent created by the external contour of the bone.

All thickness data were collected using Mitutoyo digital sliding calipers whose arms were modified to accommodate a series of interchangeable extensions, cut in a variety of shapes and sizes. This configuration provided sufficient flexibility to enable reliable measurement of all skulls. Each measure-

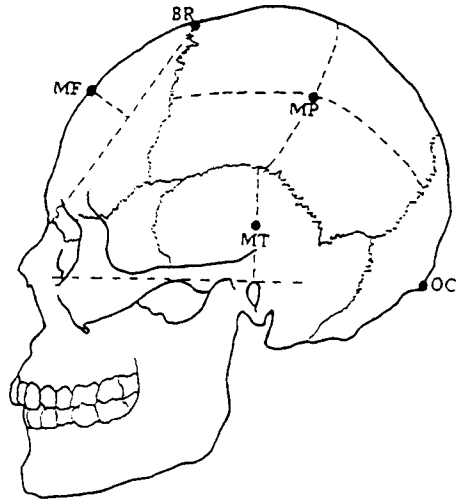


Fig. 1. Cranial thickness measurement points. See text for explanation.

ment was repeated three times; the mean of these was rounded to the nearest 0.1 mm and recorded as a data point. When possible, measurement points lateral to the midline were taken on the left side of the cranium. Every effort was made to follow an identical measurement protocol for both the extant and fossil samples and to insure that an assumption of homology was reasonable for the use of data taken from the literature (Table 1).

### Data analysis

The basic scaling relationship between two variables is described by the power function  $y = ax^b$ , where  $a$  is the  $y$  intercept or allometric constant, and  $b$  is the slope or allometric coefficient (Huxley and Tessier, 1936). In logarithmic form the power function becomes  $\log y = \log a + b \log x$ . Several statistical line-fitting methods, which vary in their calculations and inherent assumptions, are available for analyzing a bivariate structural relationship. The literature surrounding the appropriateness of the three most commonly used techniques, reduced major axis (RMA), major axis (MA), and least squares regression (LSR), is voluminous and contentious (e.g., McArdle, 1988; Martin and Barbour, 1989; Harvey and Pagel, 1991; Aiello, 1992; Hartwig-Scherer and Martin,

TABLE 2. Mean body mass (kg) and cranial thickness (mm) data for extant sample

	N F(M)	BM $\bar{X}$ (std)	MF $\bar{X}$ (std)	BR $\bar{X}$ (std)	MP $\bar{X}$ (std)	MT $\bar{X}$ (std)	OC $\bar{X}$ (std)
Cercopithecoidea							
<i>Cercopithecus</i>	21 (22)	4.8 (1.8)	1.6 (0.3)	2.0 (0.6)	1.2 (0.3)	2.6 (0.9)	3.4 (1.0)
<i>Colobus</i>	5 (7)	8.6 (1.8)	2.1 (0.4)	2.0 (0.5)	1.6 (0.3)	3.9 (1.2)	6.1 (2.1)
<i>Macaca</i>	4 (4)	9.5 (2.7)	2.0 (0.3)	2.5 (0.6)	1.7 (0.2)	3.4 (1.0)	6.6 (1.5)
<i>Papio</i>	20 (25)	18.9 (5.3)	2.6 (5.3)	3.3 (0.8)	2.9 (0.5)	4.3 (1.3)	8.6 (2.7)
Hominoidea							
<i>Gorilla</i>	7 (10)	123.5 (46.4)	7.0 (1.4)	14.9 (10.2)	5.2 (1.4)	10.4 (1.7)	34.2 (14.8)
<i>Homo</i>	13 (14)	55.9 (7.3)	7.1 (1.1)	7.6 (1.6)	7.0 (1.2)	3.7 (0.9)	14.0 (2.7)
<i>Hylobates</i>	19 (28)	5.9 (0.7)	1.6 (0.3)	1.9 (0.5)	1.3 (0.3)	3.3 (0.8)	3.8 (0.9)
<i>Pan</i>	8 (7)	41.0 (7.0)	4.1 (0.8)	4.9 (0.8)	4.2 (0.7)	8.8 (2.4)	7.5 (0.9)
<i>Pongo</i>	8 (5)	60.3 (24.1)	6.3 (1.4)	9.4 (4.5)	4.9 (1.2)	11.8 (4.5)	13.9 (3.8)
<i>Symphalangus</i>	3 (3)	11.0 (1.2)	1.9 (1.2)	2.2 (0.2)	2.0 (0.4)	3.7 (0.9)	5.1 (0.6)

1992; Smith, 1994b). To some extent, the choice of analytical method is dependent on the type of question being addressed, because each model presents application-specific advantages (Seim and Saether, 1983). RMA and MA are symmetrical structural (Model II) techniques which assume that error variance is distributed in both the dependent and independent variables. Their use is considered most appropriate when the goal of the analysis is to portray the central tendency or analyze the biomechanical relationship of a bivariate distribution (Aiello, 1992; Smith, 1993b). Least squares regression (LSR) is an asymmetrical (Model I) technique that assumes error variance is distributed only in the dependent variable. Its use is advocated when the study entails prediction or an analysis of residual data (Harvey and Pagel, 1991; Smith, 1994b). In practice when correlation coefficients are high ( $>0.90$ ), as they are for most of the variables considered here, the various analytical methods will provide negligibly different results.

The first goal of this study is to describe the empirical relationship between cranial thickness and body weight in the modern sample. This is addressed by analyzing the total catarrhine reference sample and a taxonomically narrower hominoid sample, using the LSR, RMA, and MA techniques. Application of all three methods to the data provides a means of comparing their results. However, because the objective of the analysis is to portray the functional relationship between size and cranial thickness, RMA results are emphasized in the discussion.

The second goal is to compare the individ-

ual bone thickness:body mass relationship of the three hominid species to the allometric profile of the modern sample. The position of the three hominid taxa is assessed visually, by plotting their individual data points onto the least squares regression for each variable, and quantitatively, by comparing the residuals, calculated as the difference between observed and expected values, for each data point. Residuals for *A. africanus* and *H. erectus* are constructed using predicted thickness values generated from the LSR data. The residual data, representing variance in bone thickness not accounted for by variance in body weight, are also used to evaluate the distribution of relative thickness throughout the cranium for all taxa. This is accomplished by standardizing the residual data for each variable following Smith (1984). Standardizing the residual data renders it more easily comparable by effectively converting each regression slope to a line equaling zero and registering the distribution of observations in terms of standard deviations from this line. The standardized residuals are graphed for each taxonomic unit, and these data are used to identify any patterns in the distribution of relative thickness that distinguish taxonomic groups.

To mitigate the bias that can be introduced by over-representation of particular phylogenetic groups (Smith, 1994a), all analyses use  $\log_{10}$  transformed means for each genus represented in the sample (Tables 2, 3). This procedure is followed with two exceptions. First, for obvious reasons of comparison, *H. erectus* and *H. sapiens* are considered separately. Second, because there is a more than twofold difference in the mean body weight

TABLE 3. Mean body mass (kg) and cranial thickness (mm) data for fossil hominids

	BM	MF	BR	MP	MT	OC
<i>A. africanus</i>	40.5 <sup>1</sup>	6.7	6.1	6.3	5.7	11.2
<i>H. erectus</i>	48.0 <sup>2</sup>	8.4	9.1	10.5	6.6	19.3

<sup>1</sup> McHenry, 1992.<sup>2</sup> Rightmire, 1986.

of large and small species, *Hylobates* is broken into two taxonomic units, with larger-bodied *H. syndactylus* classified separately under the now subsumed nomen *Symphalangus*.

Because of the difficulties involved in accurately estimating the gender of individual fossils, the analyses are based on pooled sex data. Most of the *A. africanus* specimens are too fragmentary for such a consideration. Even in the relatively complete crania of the *H. erectus* sample, sex determination is problematic, without associated postcranial material. Multivariate statistical techniques can be used to assess the gender of individual skulls from known populations. However, when population profiles are lacking, assignment is usually based on discrete features, such as bone thickness, robust marking, and overall size (Steele and Bramblett, 1988). In this study, dividing the fossils on the basis of these attributes would inevitably lead to circularity. Nevertheless, gender composition of the data sets is important to consider, because the outcome of the analyses will be affected by fossil samples with heavily biased sex ratios. Eighteen of the 25 Asian crania included in this study have been sexed by Weidenreich (1943, 1951); eight were classified as females, 10 as males. This assessment suggests that the *H. erectus* sample is not markedly distorted by overrepresentation of one gender, and the use of sample means approximates the species' average.

## RESULTS

The analyses show that there is strong covariance between vault thickness and body mass in both the catarrhine and hominoid samples (Table 4). Correlation coefficients for four of the five variables (MF, BR, MP, OC) are uniformly high at both taxonomic levels, ranging from 0.94 to 0.97. The

single exception occurs in temporal squamous thickness (MT), where analysis of the extant data yields lower, but still moderately strong, correlation values for both samples ( $r_{\text{cat}} = 0.83$ ;  $r_{\text{hom}} = 0.75$ ). As would be expected, the scaling data from the LSR, RMA, and MA analyses do not show significant differences for the four variables highly correlated with body mass. Confidence limits calculated for the slopes generated by the different line-fitting techniques (Sokal and Rolfe, 1981) are virtually identical for each variable and always encompass all three values. This is particularly relevant in analyses based on the total sample, where the increased number of data points produces narrower, and thus more meaningful, 95% intervals than analyses based on the smaller hominoid sample. Because of its lower correlation, confidence limits for the MT variable are broad for all analyses, and there is greater disparity in the slope and intercept values produced by the three techniques.

Overall, the scaling data are consistent between variables, especially when the results of the RMA analyses, which are not affected by differences in correlation, are compared (Aiello, 1992). Because the bivariate analyses are comparing linear and volumetric values, principles of theoretical geometric scaling would predict a slope of 0.33 if bone thickness and body weight share a 1:1, or isometric, relationship. However, the RMA slope values are all considerably higher, ranging between 0.48 and 0.62. Moreover, in all but three of the 10 RMA analyses ( $MP_{\text{hom}}$  and  $MT_{\text{cat, hom}}$ ), isometry falls outside the 95% confidence limits of the slope. Thus, the functional relationship between body size and all thickness measures appears to be positively allometric. The two midline measures (BR, OC), which incorporate crest development in the sagittal and nuchal areas, show the strongest positive relationship with body weight, with slope values ranging between 0.62 and 0.71. Scaling coefficients for the two superior vault squamous variables (MF, MP) are virtually identical ( $b = 0.55$ – $0.57$ ), while MT squamous thickness exhibits the lowest slope values in both subsamples ( $b = 0.48$  and  $0.51$ ). Removal of *H. sapiens* (see below) from the MT analyses does not alter the RMA scaling

TABLE 4. Cranial thickness regression data

Variable	Sample	r	Least squares regression				Reduced major axis			Major axis		
			SEE	Slope	Int	95% C.L.	Slope	Int	95% C.L.	Slope	Int	95% C.L.
MF	Cat	0.97	0.066	0.53	-0.199	0.43-0.64	0.55	-0.219	0.44-0.65	0.54	-0.208	0.44-0.65
	Hom	0.97	0.084	0.55	-0.234	0.35-0.76	0.57	-0.264	0.36-0.78	0.56	-0.249	0.37-0.80
BR	Cat	0.98	0.076	0.65	-0.256	0.53-0.77	0.67	-0.277	0.55-0.79	0.66	-0.269	0.55-0.79
	Hom	0.98	0.081	0.70	-0.330	0.50-0.90	0.71	-0.353	0.51-0.91	0.71	-0.345	0.52-0.94
MP	Cat	0.97	0.084	0.55	-0.285	0.43-0.69	0.57	-0.297	0.45-0.69	0.56	-0.284	0.44-0.69
	Hom	0.94	0.105	0.53	-0.232	0.27-0.79	0.55	-0.281	0.30-0.82	0.54	-0.255	0.30-0.85
MT	Cat	0.83	0.138	0.40	0.168	0.18-0.62	0.48	0.063	0.26-0.70	0.43	0.134	0.21-0.69
	Hom	0.75	0.191	0.39	0.199	-0.09-0.86	0.51	0.003	0.04-0.99	0.43	0.134	-0.05-1.18
OC	Cat	0.94	0.112	0.58	0.153	0.41-0.76	0.62	0.102	0.44-0.80	0.60	0.126	0.43-0.81
	Hom	0.94	0.129	0.66	0.004	0.34-0.98	0.70	-0.055	0.38-1.02	0.68	-0.034	0.39-1.09

data. However, it does produce an increase in the correlation values for this variable ( $r = 0.96_{\text{cat}}$  and  $0.95_{\text{hom}}$ ), which in turn produces greater accord between the RMA, LSR, and MA results.

The regression plots (Fig. 2) and residual data (Table 5) show that *H. sapiens* falls close to the primate regression for the two measures of thickness on the midline of the skull, BR and OC; however, for measures of squamous vault thickness, modern humans are only moderately well accommodated by the regression parameters of the catarrhine sample. MF and MP thickness exhibit the highest residual values of the extant series (0.12 and 0.17), and both data points are located at the upper limits of the 95% confidence intervals of the LSR slope. This suggests that, in comparison to nonhuman primates, *H. sapiens* is characterized by relatively thick bone in the superior squamous vault. The MT data point, which lies well outside and below the confidence limits of the regression, and its extremely high residual (-0.30) unequivocally identify modern humans as an outlier and denote the presence of an extremely thin temporal squama in this species.

Based on a body weight estimate of 40.5 kg, *A. africanus* displays a cranial thickness:body mass pattern that is strikingly similar to that of modern humans. Three of the five data points (MT, BR, OC) lie within the confidence limits of the catarrhine slope, and Figure 2 shows that the position of most data points approximates *H. sapiens*. Moreover, residual values for this species are strikingly similar to modern humans for all variables except MT thickness, where rela-

tive thinning of the squama is not as exaggerated.

In contrast, the cranial thickness:body mass data for Asian *H. erectus*, which are based on a body weight estimate of 48.0 kg, are distinctive relative to the two other hominid species, and nonhuman primates, as well. Four of the five thickness variables fall on or outside the confidence limits of the LSR slope (MF, MP, BR, OC). The residual values for *H. erectus* emphasize its unique position. For example, MP thickness displays the highest residual of any individual data point in the analyses (0.39). If this value reflects an accurate portrayal of their bone thickness:body mass relationship, it would suggest that *H. erectus* is characterized by relative parietal thickness which is approximately double that of *A. africanus* and *H. sapiens*, and more than 10 times greater than the relative thickness of most of the primate genera. The residual values for BR (0.12) and OC (0.16) also exhibit disparity relative to the extant sample, for they suggest that relative thickness in the midline of the *H. erectus* cranium exceeds that of all other primates, including gorillas.

Examination of the graphs portraying the distribution of relative thickness throughout the skull in each taxon reveals that cercopithecoid and small-bodied hominoid genera are all characterized by low standardized residual values (Fig. 3). The single exception occurs with *Cercopithecus*, which displays substantial relative thickness at bregma. The large-bodied apes exhibit greater variability, especially in BR and OC, where development of the sagittal and nuchal crests produces relative thickening in the cranial



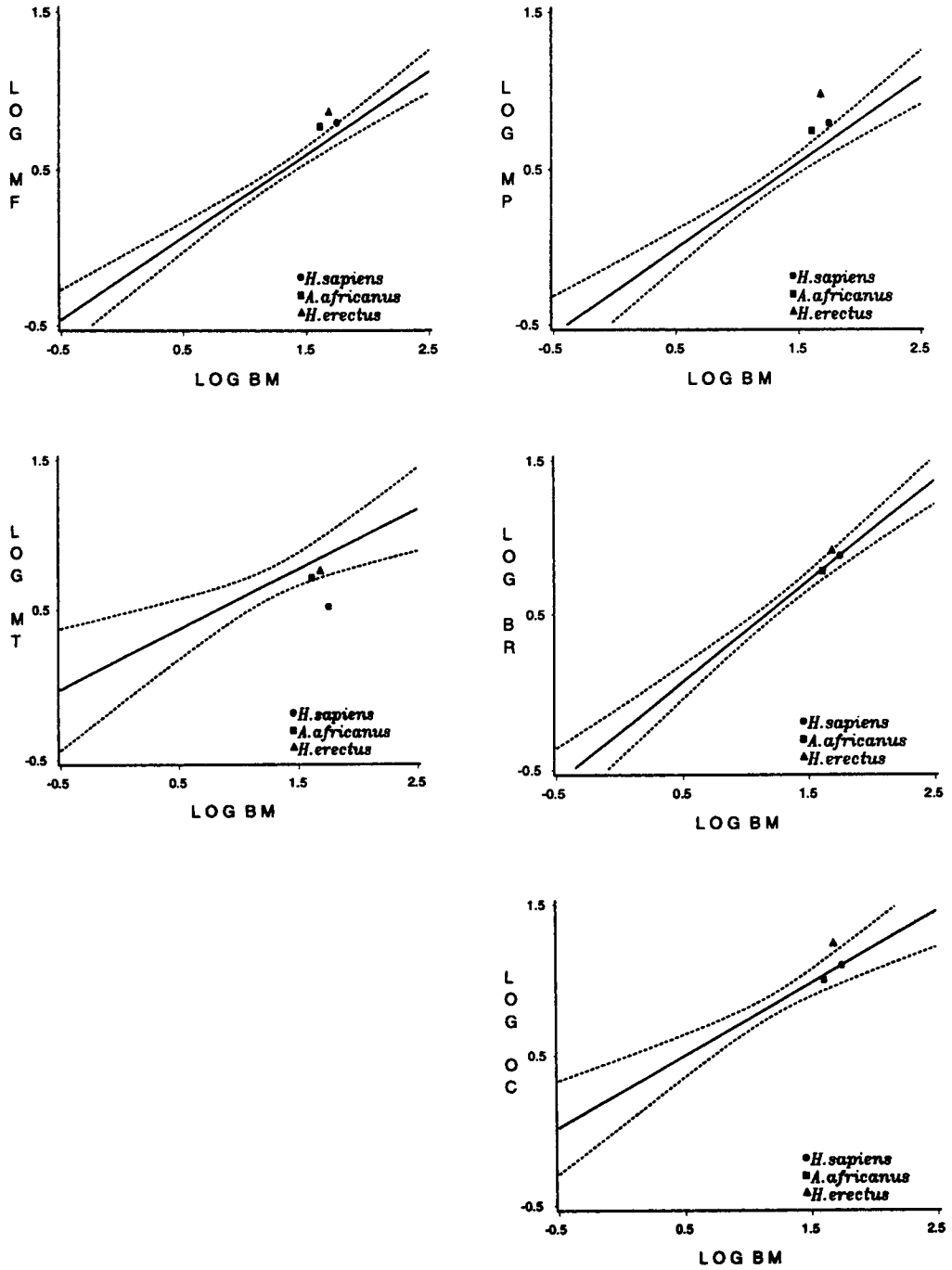


Fig. 2. Location of hominid data points in relation to catarrhine least squares regression for five cranial thickness variables. Dashed lines represent 95% confidence limits of LSR slope. See Table 4 for regression data.

TABLE 5. Primate and fossil hominid  $\log_{10}$  residuals calculated from least squares regression data for catarrhine sample

	MR	BR	MP	MT	OC
Cercopithecoidea					
<i>Cercopithecus</i>	0.04	0.11	-0.02	-0.03	-0.02
<i>Colobus</i>	0.03	-0.04	-0.02	0.05	0.09
<i>Macaca</i>	-0.01	0.02	-0.03	-0.02	0.10
<i>Papio</i>	-0.06	-0.05	0.05	-0.04	0.04
Hominioidea					
<i>Hylobates</i>	0.00	0.04	-0.03	0.04	-0.02
<i>Symphalangus</i>	-0.07	-0.08	0.02	-0.02	-0.05
<i>Pan</i>	-0.04	-0.10	0.03	0.13	-0.22
<i>Gorilla</i>	-0.77	0.07	-0.15	0.01	0.17
<i>Pongo</i>	0.05	0.07	-0.01	0.19	-0.04
Hominidae					
<i>H. sapiens</i>	0.12	0.01	0.17	-0.30	-0.02
<i>A. africanus</i>	0.17	-0.01	0.20	-0.05	-0.04
<i>H. erectus</i>	0.22	0.12	0.39	-0.04	0.16

midline for *Pongo* and *Gorilla*. It is especially important to note the distribution of relative thickness in the squamous portions of the vault of *Pongo* and the African apes. In comparison to the superior squamous vault (MF, MP), all three taxa are characterized by increased relative thickness in the inferior region of the skull (MT).

In contrast, all three hominids display a consistent, and distinctive, pattern in the distribution of their relative thickness throughout the cranial vault. The scaling data for *H. sapiens* and *A. africanus* have already suggested a profile of this pattern, which is characterized by relative thickening of the frontal and parietal squama and relative thinning of the temporal squama. What is most strikingly displayed by the graphs in Figure 3, but was not readily apparent in the scaling analyses, is the almost complete identity, in the distribution of its relative thickness, of *H. erectus* to the two other hominid species. The only notable difference occurs in the relationship between the lines representing the standardized residuals and the regression slope. Here the large absolute cranial thickness values of *H. erectus* produce a "frame shift" in the residual data.

## DISCUSSION

Several studies have addressed the significance of differences in cranial bone thickness in modern *H. sapiens*. The strong covariance between extant primate body size and cranial thickness, as well as its positive allo-

metric relationship, are similar to patterns documented for postcranial bone thickness across a broad range of vertebrates, including primates (Biewener, 1982; Ruff, 1987, 1990; Selker and Carter, 1989; Anyonge, 1993; Nelson, 1994). In the postcranium this relationship is usually considered a byproduct of the functional interaction between mass and skeletal support. While this may be so, the cranial data demonstrate that the association between mass and thickness is also expressed in non-weight-bearing portions of the skeleton. The strength of the association suggests that, at the interspecific level, measures of bone thickness throughout the skeleton covary primarily in relation to size, with specific biomechanical influences exhibiting secondary, localized influences. It is possible that this covariance is established and maintained through the pleiotropic effects of genetically mediated growth hormone systems that target coordinated growth of the entire organism (Nelson and Gauld, 1994; Shea, 1992). The interaction between mass and cranial thickness, and its effects on intragroup variation, have not been carefully investigated in any primate species. However, a relationship between size and thickness can be found in support for human developmental studies, which show steady, rapid thickness increases during growth (Roche, 1953; Adeloje et al., 1975; Brown et al., 1979). Moreover, in measuring the effects of sex, age, race, height, and weight on cranial thickness in a large cadaver sample, Pensler and McCarthy (1985) demonstrate that only weight covaries consistently, and significantly, with thickness. The lower correlation values shown in their study ( $r = 0.29-0.69$ ) are not unexpected, given the increased number of environmental factors contributing to individual phenotypic thickness variation.

The results indicate that caution should be exercised in treating absolute values of cranial bone thickness as diagnostic phylogenetic traits because they do not satisfy a criterion of independence. However, careful analysis of traits that share a strong relationship with size can reveal phylogenetically meaningful information. Examination of the distribution of relative thickness throughout the cranium shows that *A. afri-*

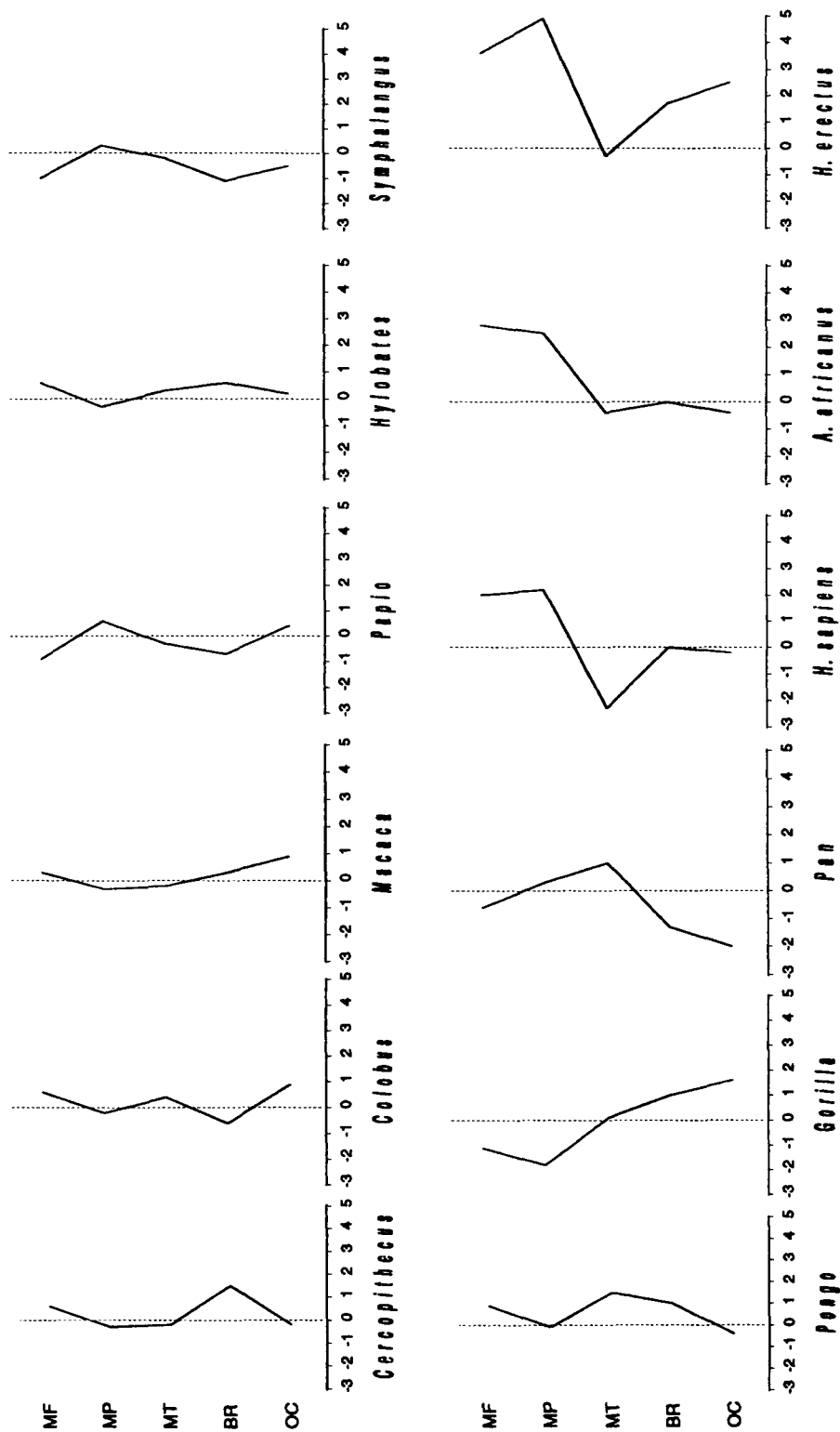


Fig. 3. Distribution of relative cranial thickness throughout the cranium in each modern genus and fossil species. Dashed line represents least squares regression slope; solid line plots standardized residuals for each data point.

*canus*, *H. erectus*, and modern *H. sapiens* share a consistent profile that is distinguishable from nonhuman taxa. This suggests that the distribution of relative thickness may be taxonomically relevant, perhaps in diagnosing membership in the family Hominidae, or possibly, if alternate character states are identified for other hominid species, in diagnosing relationships within the family.

The distinctive patterns characterizing hominid and nonhominid species in their distribution of relative thickness throughout the skull need to be addressed from a structural-functional perspective as well. Although they account for a very small portion of the overall variance, the consistency of the different patterns suggests that these groups are responding to different functional constraints. One explanation for these patterns is that they reflect an interaction between cranial form and biomechanical stress. The idea that there is a relationship between cranial thickness, cranial form, and biomechanics is not new. In his analysis of the *Sinanthropus* skull, Weidenreich (1943) proposed that the architecture of the *H. erectus* cranium provides a structural reinforcement system by the development of thick bone and buttresses, in the form of keels and tori. He argued that the decrease in the absolute dimensions of cranial thickness between modern *H. sapiens* and *H. erectus* was directly related to an increase in brain size and the formation of a more globular calvarial shape. With the australopithecine data now available, it is clear that no inverse relationship between brain size and vault thickness exists within the family Hominidae (Tobias, 1967). However, some support exists for Weidenreich's model, at least for its most general aspects.

Demes (1985) has examined the forces generated on the cranium in a series of primates; she concludes that vault strength increases as the shape of the cranium becomes more spherical. She also notes a correlation between vault thickness and cranial shape in mammals. Although it is clear that vault thickness, which is one measure of bone mass in the cranium, shares a primary relationship with body size, the residual data presented here suggest that species-level

changes in this relationship can be effected at localized points of the skull vault. It is likely that such changes arise as a biomechanical response to differences in masticatory forces and/or cranial vault architecture. The relationship between cranial thickness and biomechanics deserves further exploration, especially in reference to the differences that characterize hominid and nonhominid primates. One of the best methods for achieving this is to properly account for, and remove, size-related variance from measures of vault thickness.

Together, the results of the allometric and residual analyses show that Asian *H. erectus* exhibits a cranial thickness:body mass relationship that does not accord well with the scaling pattern displayed by modern catarrhines. This relationship is also dissimilar to the thickness:mass relationship characterizing both the primitive hominid species *A. africanus* and modern *H. sapiens*. However, in their distribution of relative thickness throughout the cranial vault, all three hominid species share a common pattern. It is possible that, in *H. erectus* and other thick-boned Pleistocene hominids, there has been a disruption of the covariance and scaling relationship that describes modern primates and the two hominid species. The results of the allometric analyses cannot invalidate the presence in these groups of some selective mechanism for thick bone that produces a deviation from the size-related relationship observed in other species. However, the results do delineate a number of conditions which must be addressed by any explanatory model postulating such a mechanism. First, any selective mechanism invoked as an explanation for thickened bone must be one which accommodates and incorporates the maintenance of one pattern and the disruption of another. Second, large absolute dimensions in bone thickness are present throughout the skeleton in the same early hominid populations that display thick cranial bone (Nelson et al., in press). Furthermore, as has been previously discussed, the strong covariance and scaling relationship that characterizes cranial thickness is also present in primate postcranial thickness measures. Thus, explanations for thickened bone in hominids must account for the dis-

ruption of the bone thickness:body mass relationship on a skeleton-wide level. Third, a selective mechanism for thickened bone in *H. erectus* and archaic *H. sapiens* must be adaptively distinguishable from anything that occurs among all the remaining taxa sampled in this study, despite their historical, ecological, behavioral, and morphological diversity.

Alternatively, it is possible to propose an interpretation of the allometric data for cranial thickness which is both parsimonious and uniformitarian. The disparity between the regression data for modern catarrhines and *H. erectus* would have arisen if the body weight estimate assigned to this species greatly underestimates its actual size. The use of a low body-mass estimate would produce an apparent disjunction in the scaling relationship, resulting in the large residual values which characterize these fossils. At the same time, it would not affect the pattern describing the distribution of relative thickness throughout the skull except to produce the observed "frame shift."

Estimation of body mass in fossil taxa is a difficult task, with many methodological and sampling factors influencing the final results (Jungers, 1990; Nelson et al., in press). The published body-weight estimate used in this paper (Rightmire, 1986) was taken from the only study which has systematically addressed prediction of body mass in non-African *H. erectus* populations. The results of that study have remained unquestioned, at least in part, because they satisfy an unstated expectation that a temporally intermediate hominid species should exhibit intermediate body size. The findings presented here support recent body-weight prediction studies of *H. erectus* in suggesting that Asian, as well as African, members of this species were characterized by substantially large body size (McHenry, 1988; Gauld, 1992; in preparation; Ruff and Walker, 1993; Aiello and Wood, 1994). Given the importance of size as a fundamental species adaptation and its impact on the development of lineage-specific evolutionary strategies (Maiorana, 1990), the results of this study suggest that body size in extinct populations of *Homo* needs to be studied with greater intensity.

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